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# A NEW, SIBLING SPECIES OF SNAPPING SHRIMP ASSOCIATED WITH THE CARIBBEAN SEA ANEMONE *BARTHOLOMEA ANNULATA*

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ABSTRACT

*Alpheus immaculatus*, a new species of snapping shrimp associated with the Caribbean sea anemone *Bartholomea annulata*, is described and figured. This new species, together with the well known *Alpheus armatus*, and a much rarer, as yet undescribed, third species, make up a complex of sibling species that share the same host and are extremely similar morphologically. A small set of distinctive color pattern differences unambiguously distinguishes these species when alive, and one morphological character can also be used to distinguish the two species in most preserved specimens. No reproductive pairings between species have been observed in the field. In the laboratory, adult males and females of different species behave very aggressively towards each other, in contrast to the placid interactions between conspecific, adult, male-female pairs. The distribution of *A. immaculatus* is wider with respect to depth than that of *A. armatus*. Deeper than 15 m, including all collections from anemones seaward of the reef crest, only *A. immaculatus* has been found. In many shallower backreef areas, *A. armatus* and *A. immaculatus* occur microsympatrically, although in some locations only *A. armatus* is found.

The snapping shrimp *Alpheus armatus* Rathbun is a conspicuous associate of the Caribbean sea anemone *Bartholomea annulata* (Clarke, 1955; Limbaugh et al., 1961; Smith, 1977). Small anemones often shelter single juvenile shrimp, while large clusters of anemones almost invariably contain a male-female pair of adults (Knowlton, 1978). These shrimp are strongly territorial (Knowlton and Keller, 1982).

During a study of the reproductive biology of this species in Discovery Bay, Jamaica, several different "morphs" were recognized (Knowlton, 1978, 1980). One morph, found on a patch reef in −10 m, was first noticed through the observation that some adult males lacked the typical, conspicuous blackening of the uropod spines (see Chace, 1972). Female egg color was also distinctively olive in some individuals, rather than the more usual red. A second, much less common morph, found in −3 m close to shore, also had reduced sexual dimorphism in uropod spine color, achieved, however, through both a lightening of male spines and a darkening of female spines. The major and minor chelae and third maxillipeds in this morph were also unusually spotted.

Here we report that these morphs mate in a strictly assortative fashion and must therefore be viewed as separate species. Although they are unambiguously separated when alive by a small but consistent set of color differences, they can be described as sibling species because of their largely similar color pattern, their sharing of the same anemone host, and their extreme similarity in those morphological characters retained after preservation.

Examination of the type specimen of *A. armatus* (USNM 23784) revealed that it was a male (not a female, as originally stated by Rathbun, 1900) of the abundant shallow water form with strongly sexually dimorphic uropod spines (Chace, 1972). Here we describe the new, generally deeper water species (the first of the two morphs mentioned above); description of the third, rarer species will be delayed until more specimens are available.

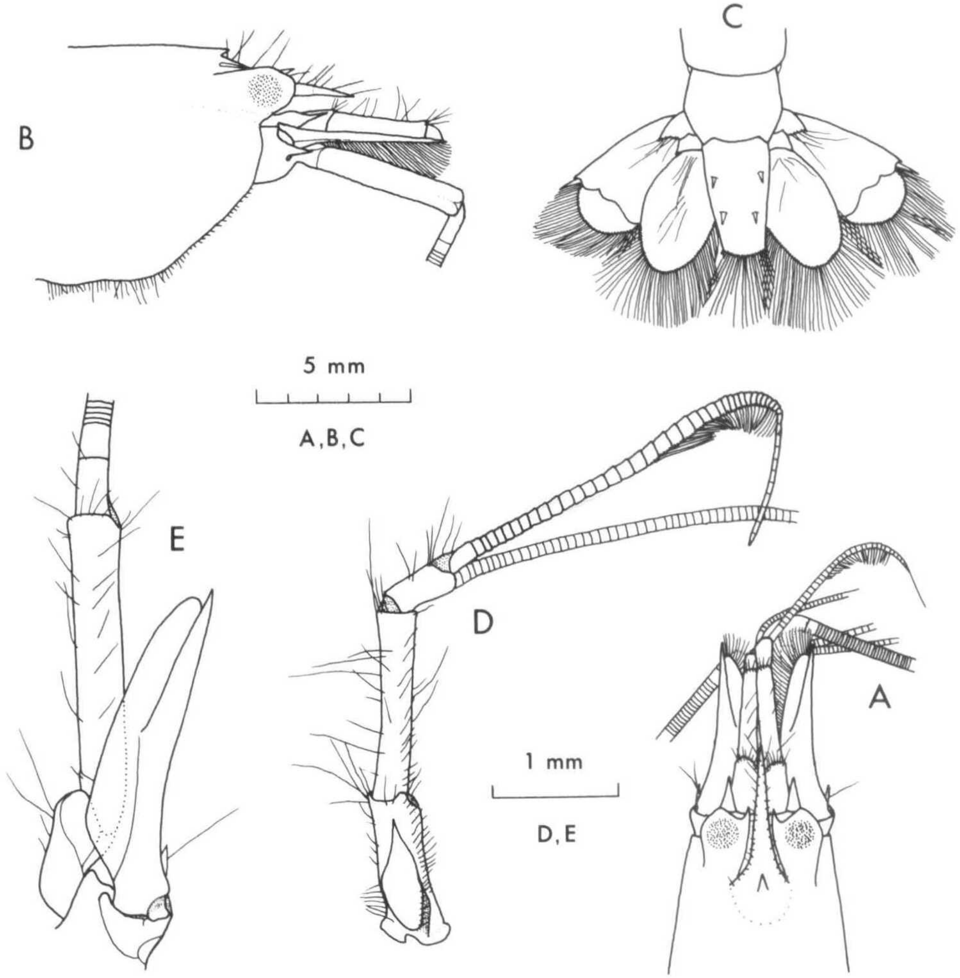


Figure 1. *Alpheus immaculatus* new species, male: A, anterior region, dorsal view; B, anterior region, lateral view; C, telson and uropods; D, right antennule; E, right antenna (setae removed from lamina of antennal scale).

## *Alpheus immaculatus* new species

*Material Examined.*—Discovery Bay, Jamaica (−5 to −15 m): 12 males (including holotype, USNM 195329), 12 females (7 ovigerous), 2 juveniles; Caracol Bay, Haiti (−2 to −23 m): 3 males, 4 females (2 ovigerous). Paratypes of adult and juvenile specimens from these localities have been deposited in the United States National Museum, the Yale Peabody Museum, and the Institute of Jamaica.

*Description.*—Rostrum (Figs. 1A, 4A) slender, tapering to point, extending to or slightly beyond anterior margin of basal segment of antennular peduncle; somewhat depressed, concave from base to tip, tip sometimes bent slightly downward (Fig. 1B); row of long setae along lateral margins. Ocular hoods (Fig. 1A, B) well produced, continuous with carapace; armed with sharp dorsomesial tooth extending to about anterior margin of hood; anterior face flattened from base of tooth to midline of hood. Variably shaped tooth (occasionally a rounded protuberance) on midline of carapace about even with base of ocular hoods. Carapace smooth, laterally compressed (height slightly less than or subequal to length);

anterior margin (Fig. 1B) nearly vertical just below ocular hood, slanting posteroventrally from near base of antennal peduncle; ventral margin fringed with fine setae, convex between coxae of first and fourth pereopods; posterior margin rounded ventrally, with cardiac notch (Chace, 1972).

Abdominal somites smooth, anterior five with broadly rounded pleura fringed with plumose setae. Sixth somite strongly concave around insertion of uropod. Telson (Fig. 1C) about two-thirds as wide as long; lateral margins slightly sinuous; posterior margin slightly more than half as wide as anterior margin; two pairs of dorsal spines, inserting roughly one-third and two-thirds down length of telson. Posterior margin of telson slightly arcuate; armed with two pairs of lateral spines, inner pair at least twice as long as outer pair; fringed with sparse upper row of setae and lower row of long plumose setae.

Eyes completely enclosed within ocular hoods (Fig. 1A, B). Cornea subspheroidal and darkly pigmented.

Antennular peduncle (Fig. 1A, D) long, slightly overreaching antennal scale; stylocerite sharply acute, extending nearly to end of first segment of antennular peduncle; second segment somewhat longer than first and at least twice as long as third. Upper, more lateral flagellum slightly stronger proximally than lower flagellum, distal 10–15 segments distinctly thinner than proximal segments; lower flagellum about three times longer than upper flagellum, extending to or beyond posterior margin of carapace.

Antennal scale (Fig. 1A, E) about four times as long as wide; lateral margin concave proximally, straightening distally to slender point; inner margin convex, fringed with long plumose setae; narrow slit extending anterolaterally along distal half of antennal scale, partially separating outer spine from inner lamina. Antennal peduncle (Fig. 1B, E) overreaching antennular peduncle (not apparent in Fig. 1A because of perspective); basal segment armed with sharp ventrolateral tooth below articulation of antennal scale, tooth not reaching tip of stylocerite; distal segment of antennal peduncle slender, about 7–8 times longer than wide, with well-developed flagellum extending posteriorly far past tip of telson.

Maxillipeds, maxillae, and mandible as shown (Fig. 2). Third maxilliped (Fig. 2A) extending nearly to tip of antennal peduncle, with numerous long setae, mesial surface of distal segment covered with tufts of short setae.

Major first pereopod (Fig. 3A, B) extending beyond antennal peduncle by much of chela. Chela compressed, ovate, and twisted, with fingers closing in plane nearly perpendicular to plane of compression of proximal part of palm; chela proportionately larger in adult males than in adult females. Fingers usually less than half length of palm; movable finger compressed and somewhat curved, opposing margin with large flattened tooth fitting into socket in fixed finger; fixed finger subconical, tip curving toward movable finger, opposing margin with small blunt tooth distal to socket. Palm with numerous tubercles and long setae on surface which grades into fixed finger; sharp marginal tooth adjacent to insertion of movable finger; paired, weakly developed tuberculous ridges on both sides of palm along plane of compression; surface from which movable finger extends smooth, with small blunt tooth adjacent to insertion of movable finger. Merus with sharp distal tooth, flexor margins weakly denticulate.

Minor first pereopod (Fig. 3C) overreaching antennal peduncle by most of chela. Movable finger subcylindrical and slightly tapering, terminating with sharp curved tooth, row of small teeth along opposing margin; fixed finger subcylindrical, sharply pointed tip, blade-like ridge opposing movable finger; fingers somewhat longer than or subequal to palm, slightly concave ventrally (perpendicular to closure plane). Males longer from rostrum to telson than about 21 mm (Jamaican spec-

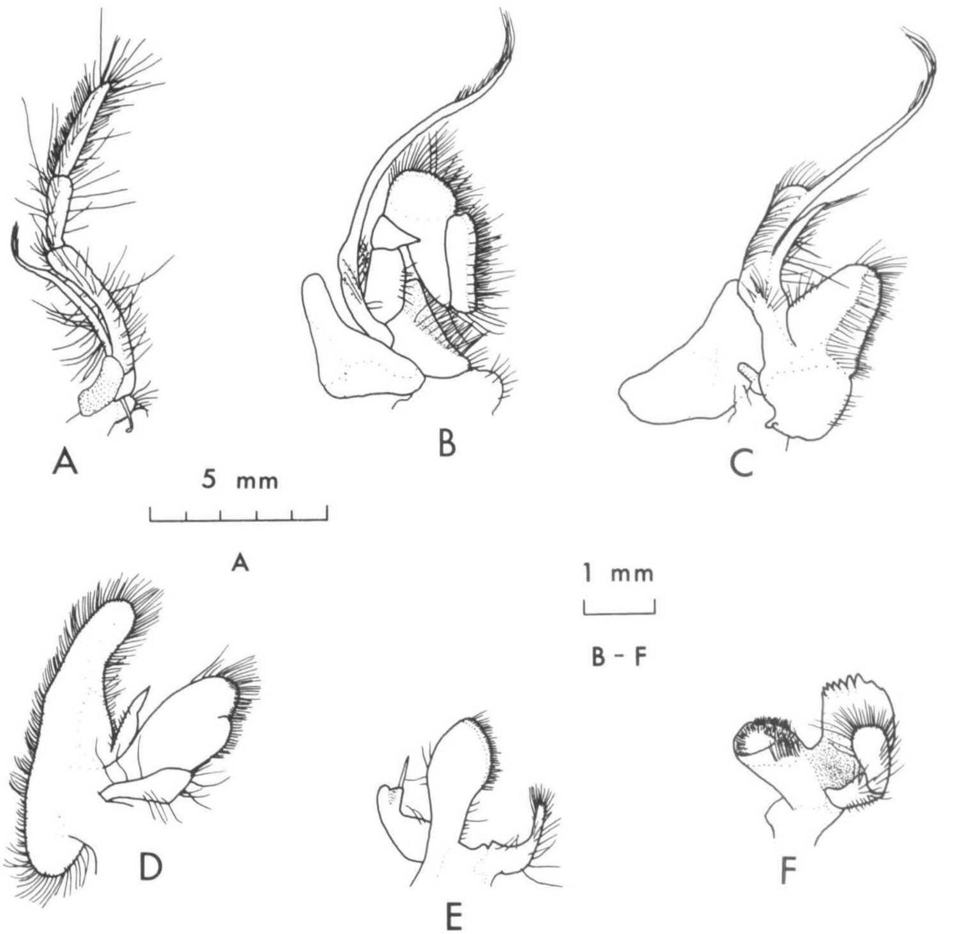


Figure 2. *Alpheus immaculatus* new species, male: A, right third maxilliped; B, right second maxilliped; C, right first maxilliped; D, right second maxilla; E, right first maxilla; F, right mandible.

imens) to 26 mm (Haitian specimens) with somewhat "balaeniceps shaped" movable finger (Banner and Banner, 1966); row of coarse, short setae extending over about proximal half of fixed finger on either side of blade-like ridge. Palm subcylindrical, distal well produced acute dorsal tooth and less produced acute ventral tooth adjacent to insertion of movable finger; surface from which movable finger extends smooth, opposite surface tuberculose with long setae. Carpus with tooth on distal extensor margin. Merus with sharp distal tooth, flexor margins weakly denticulate; longer than merus of major cheliped, subequal in width.

Second pereopod (Fig. 3D) extending past antennal peduncle by at least chela and most of carpus; fingers subequal in length to palm; carpus about four times longer than chela, subdivided into five articles, numbered 1 to 5 distally (Chace, 1972), usually decreasing in length as: 1, 2, 5, 3, 4; articles 2 and 5, and 3 and 4, frequently subequal; merus somewhat longer than proximal article of carpus and subequal to or longer than ischium. Third pereopod (Fig. 3E) overreaching antennal peduncle by dactyl and much of propodus; dactyl simple and unarmed, about one-fourth as long as propodus; propodus with two distal spines flanking

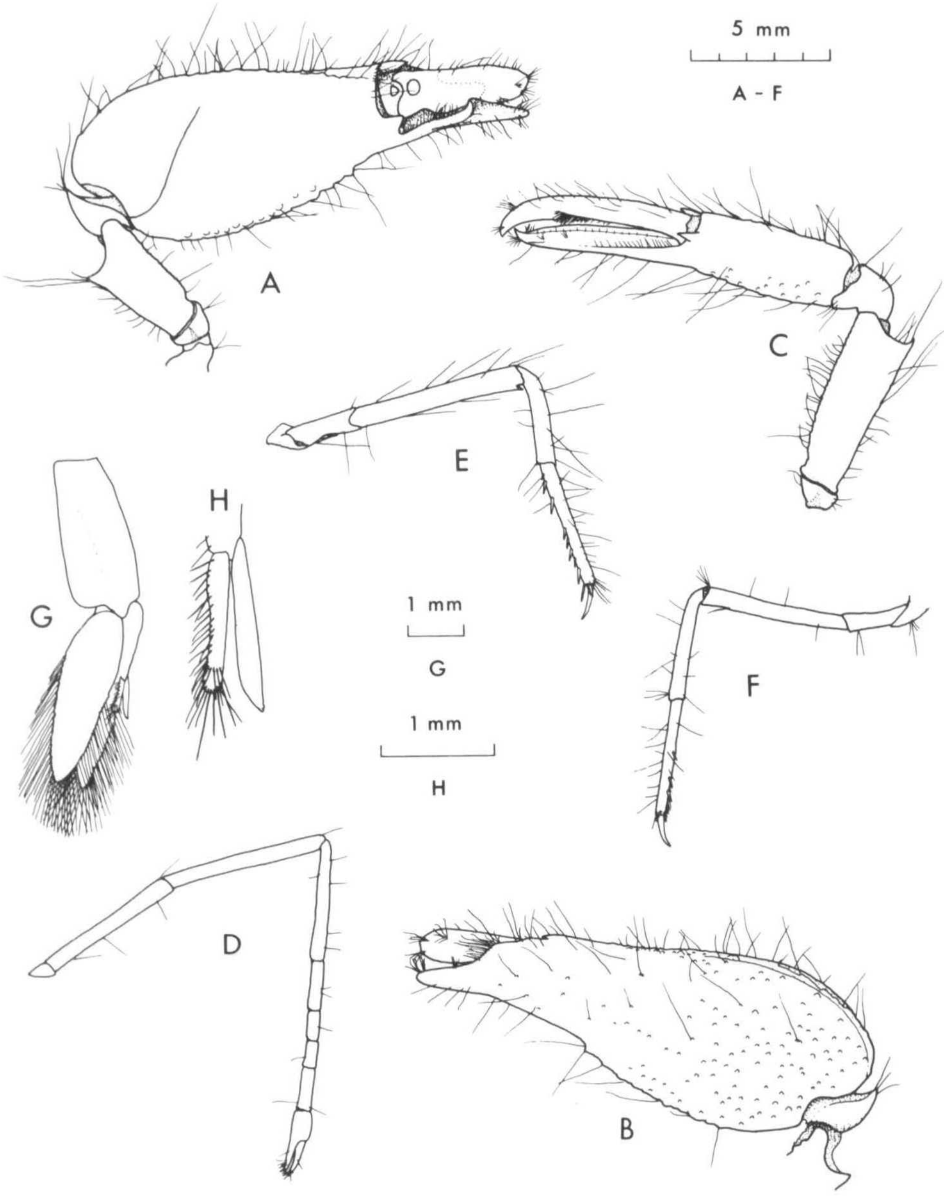


Figure 3. *Alpheus immaculatus* new species, male: A, major first pereopod (right), lateral view; B, chela of major first pereopod, mesial view; C, minor first pereopod (left); D, right second pereopod; E, right third pereopod; F, right fifth pereopod; G, right second pleopod; H, appendix masculina and appendix interna.

insertion of dactyl and series of spines along flexor margin, numbering 8–11 for males and 7–10 for females at least 16 mm long, 6–7 for smallest sexed specimens (10–13 mm), and 3–5 for small juveniles (6–7.5 mm); carpus about two-thirds as long as propodus; merus about twice as long as carpus, armed with acute tooth at distal flexor margin; ischium armed on lower face with sharp spine inserted in

oblong pit. Fourth pereopod extending past antennal peduncle by dactyl and part of propodus similar to third pereopod, except with 1–3 fewer propodal spines. Fifth pereopod (Fig. 3F) somewhat smaller than third and fourth pereopods, overreaching antennal scale by dactyl; flexor margin of propodus with 1–5 spines, additional pair of spines at insertion of dactyl; propodus with dense tuft of short setae on distal fourth; merus and ischium unarmed.

Second (Fig. 3G) to fifth pleopods similar in size and with appendices (see Chace, 1972). Appendix masculina (Fig. 3H) on second pleopod of adult males, somewhat shorter than or subequal to appendix interna. Pleopods of reproductive females (at least 22 mm long) with more setae than those of males. Smallest ovigerous female (22 mm long) with 43 ova early in development. Largest (37 mm) with 229 ova late in development. Additional female lengths and ovum numbers: 23 mm, 209 ova; 27.5 mm, 291 ova; 29.5 mm, 471 ova; 30 mm, 155 ova; 34 mm, 471 ova; and 35 mm, 317 ova. Ova change in color, size, and shape during development; early, subspheroidal to oblong (mean $0.68 \times 0.60$ mm, N = 8), light orange (preserved); late, oblong (mean $1.43 \times 0.75$ mm, N = 8), laterally compressed, with darkly pigmented eyes and clearly defined abdomen coiled anteriorly past rostrum.

Uropods (Fig. 1C) subequal in length and somewhat longer than telson; lateral branch with tri-lobed transverse suture near distal margin, long slender spine inserting between two acute teeth at lateral end of suture, short row of setae distal to innermost tooth; mesial branch oblong, unarmed, with group of setae along midline. Distal margins of uropods fringed with upper row of setae and lower row of long plumose setae.

*Coloration in Life.*—Adults have red and white striped antennae, while juveniles (<10 mm rostrum–telson length) have entirely white antennae or white antennae with red tips. The body pattern of adults is a complex arrangement of translucent, white and red patches. Most easily described are the dark, eye-like markings on the sides of the second and third abdominal somites, and the absence of red pigment down most of the dorsal midline of the abdomen. See Kaplan (1982, plate 29, no. 3) or Zeiller (1974, p. 76, misidentified as *A. formosus*) for color photographs of the overall very similar *A. armatus.* The color pattern of juveniles changes as length increases. The smallest juveniles (6–6.5 mm) are faintly reddish-orange, and most have whitened corneas and a fairly straight, opaque, white stripe along the dorsal midline of the carapace and abdomen. Larger juveniles (7–10 mm) have darker red-orange bodies and a straight white stripe, but no longer have whitened corneas. With increasing size, the midline stripe becomes less pigmented with white, particularly along the posterior region of the carapace.

*Measurements (in mm).*—Total length: males 10 to 37.5 (holotype 31.5, figured specimen 28.5), females 9 to 37, juveniles 6.5 and 7.5. Carapace length: males 3.5 to 12.5 (holotype 10, figured specimen 9), females 3.5 to 11.5, juveniles both 2.5. Length of propodus of major first pereopod: males 4 to 20 (holotype 17, figured specimen 12), females 4.5 to 17, juveniles 2 and 2.5.

*Type Locality.*—East Discovery Bay, Jamaica, near the central harbor buoy at approximately −10 m, from the anemone *Bartholomea annulata.*

*Etymology.*—The name "immaculatus" is taken from the Latin for spotless, referring to the absence of green spots which distinguishes the species when alive.

*Color Differences between* A. immaculatus *and* A. armatus.—The feature which reliably distinguishes all size and sex classes of *A. immaculatus* from *A. armatus*

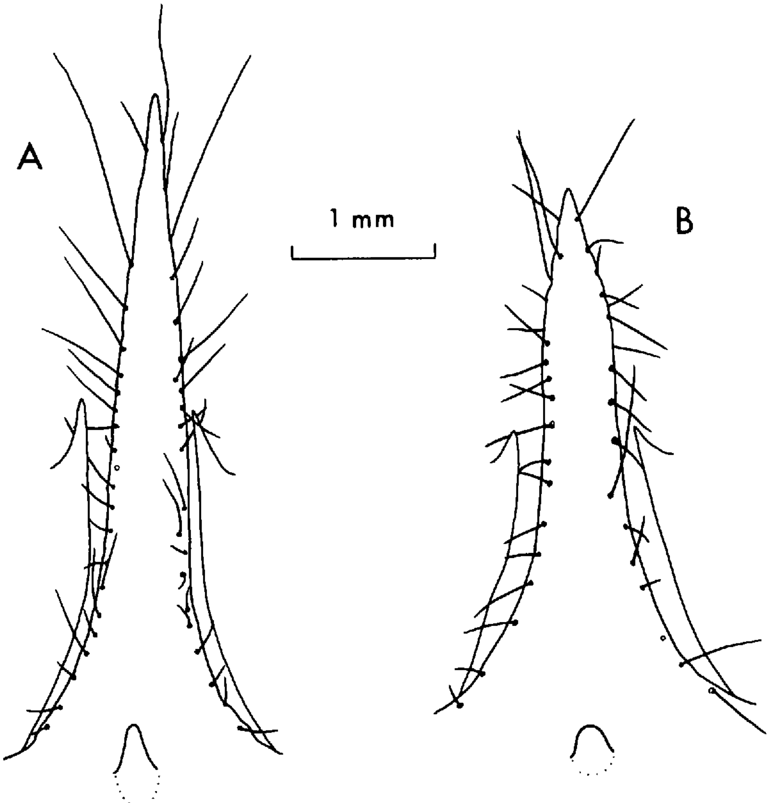


Figure 4. Rostrum of: A, *Alpheus immaculatus* new species, male, total length 28.5 mm; B, *Alpheus armatus* Rathbun, male, total length 29 mm.

is the absence of iridescent green spots. In *A. armatus* these are found on the antennular peduncles, and in single lines along the inner surfaces of the first chelipeds and down the dorsal midline of the carapace and abdomen. In *A. immaculatus* there are generally no green spots, although sometimes there is a light flush of green on the antennular peduncles, and in a few specimens we found a single green spot on the major cheliped. (The third species in this complex is characterized by a profusion of these green spots anteriorly.)

Several other color differences distinguish certain size-sex categories. First, the antennae of juvenile *A. armatus* are striped as in the adult, while a full set of red antennal stripes does not begin to develop in *A. immaculatus* until a rostrum–telson length of approximately 15 mm is reached. Second, juveniles differ in the pattern of opaque white pigmentation along the dorsal midline of the carapace. *A. armatus* juveniles quickly lose the continuous white stripe down the dorsal midline; when 7–8 mm long they develop a diamond-shaped patch of white centered around the carapace tooth posterior to the rostrum and lose the white pigment along most of the rest of the carapace; this white diamond remains evident for individuals at least 14 mm long. *A. immaculatus* in the size range of 7–14 mm retain, instead, the continuous white stripe along the dorsal midline of the carapace. Third, as mentioned above, the yolk of the eggs is olive in *A. imma-*

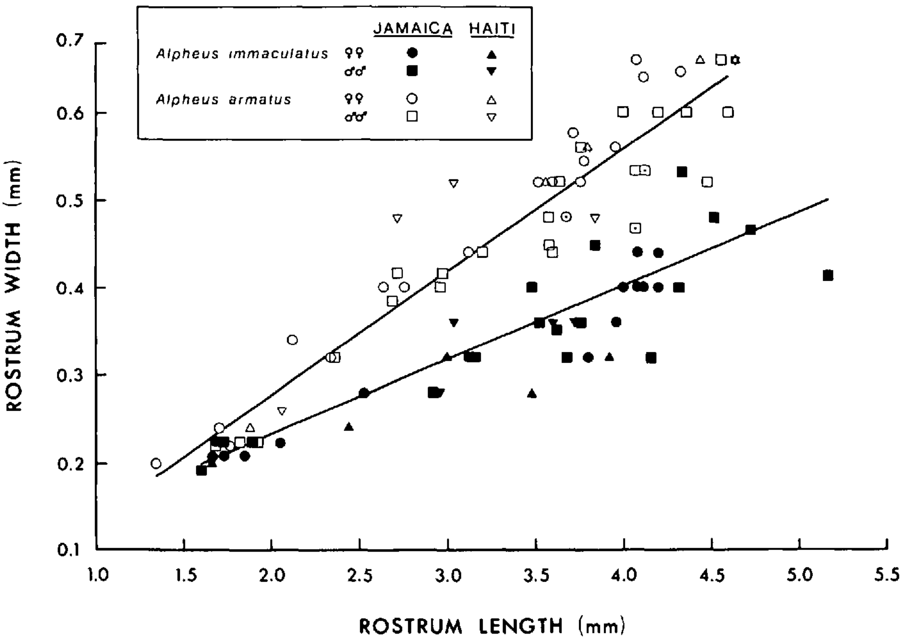


Figure 5. Relationship between rostrum length and width for *Alpheus immaculatus* new species, and *Alpheus armatus* Rathbun. Lengths were measured from the basal median tooth to the distal tip, and widths were measured at the level of the tips of the teeth arising from the ocular hoods (see Fig. 4). Linear regressions for males and females of each species had similar slopes ($P > 0.05$, analyses of covariance) and were pooled for a comparison of slopes between species, which was highly significant ($P < 0.001$, analysis of covariance). The regression equations are: $Y = 0.084X + 0.065$ ($N = 35$) for *A. immaculatus* and $Y = 0.140X - 0.003$ ($N = 42$) for *A. armatus*; both regressions are based on Jamaican specimens only. Open symbols enclosing a small solid point indicate specimens of *A. immaculatus* and *A. armatus* which had the same measurements for rostrum length and width.

*culatus* and red in *A. armatus*. Finally, adult males of *A. immaculatus* have uropod spines with nearly clear cuticles and pigmented internal tissues which blend with the overall reddish color of the uropods; the spines resemble those found on females of both *A. immaculatus* and *A. armatus*. In adult males of *A. armatus* the cuticle of these spines is conspicuously blackened, obscuring the internally colorless tissues (except in recently molted individuals whose white spines gradually darken over several days).

Unfortunately, most of these color differences disappear soon after preservation. Only the cuticular blackening of the uropod spines in adult male *A. armatus* is retained as distinctive in preserved specimens more than several years old, and even this character is not reliable in very old specimens (e.g., the type).

*Anatomical Differences between* A. immaculatus *and* A. armatus.—A skeletal character which distinguishes most specimens of *A. immaculatus* from *A. armatus* is the shape of the rostrum (Fig. 4). *A. immaculatus* generally has a longer, more slender rostrum than *A. armatus* (Fig. 5), except for specimens less than about 15 mm long.

In addition to the distinctive cuticular blackening of the uropod spines of adult male *A. armatus*, the spines are larger than those of female *A. armatus*, and both male and female *A. immaculatus*. For specimens longer than about 30 mm, this size difference typically is about two-fold for both spine length and basal width.

Table 1. Contingency tables showing the absence of interspecific male-female pairs (*A. immaculatus* with *A. armatus*) at locations in Discovery Bay, Jamaica where the two species occur microsympatrically. See Knowlton (1980) for a map of Discovery Bay showing the exact location of the northeastern site (SAII). *A. imm.*: *A. immaculatus*, *A. arm.*: *A. armatus*

| Region of Discovery Bay | Depth (m) | Males | Females | |
|---|---|---|---|---|
| | | | *A. imm.* | *A. arm.* |
| Northwest | 3–9 | *A. imm.* | 23 | 0 |
| | | *A. arm.* | 0 | 21 |
| West | 4–16 | *A. imm.* | 36 | 0 |
| | | *A. arm.* | 0 | 58 |
| East | 5–19 | *A. imm.* | 17 | 0 |
| | | *A. arm.* | 0 | 2 |
| Northeast (SAII) | 10 | *A. imm.* | 8 | 0 |
| | | *A. arm.* | 0 | 2 |

*Distributional Differences between* A. immaculatus *and* A. armatus.—In our collections around Discovery Bay, Jamaica, and Caracol Bay, Haiti, *A. immaculatus* was the only species of alpheid found with *B. annulata* at depths greater than 15 m. Since this anemone appears to be intolerant of high surge, most anemones seaward of a fringing reef crest are at these depths; hence on the forereef only *A. immaculatus* has been found. In more protected areas behind the reef crest, the distributional pattern is more complex, and the two species are often sympatric on a scale of meters. In the shallowest areas (<4 m) one can find either no *A. immaculatus* (east Discovery Bay) or a mixture of the two species (west Discovery Bay, Caracol Bay). At greater depths in backreef lagoons, the relative abundance of *A. immaculatus* increases. Thus the distribution of *A. immaculatus* is wider with respect to depth than that of *A. armatus.*

*Evidence for the Absence of Potential Interbreeding.*—We have two types of evidence which suggest that interbreeding between *A. immaculatus* and *A. armatus* is rare or absent. First, in areas of sympatry no interspecific male-female pairs have ever been found, even in locations where one species was comparatively rare. This pattern is summarized in Table 1 for areas from which we have adequate collections containing both species.

Second, in the laboratory it is easy to establish male-female pairs between conspecific adults (as evidenced by the sharing of a cluster of anemones) and impossible to do so between heterospecific adults, which interact aggressively. In four intraspecific male-female pairings between individuals greater than 30 mm in length, no snaps were exchanged and no injuries occurred. In five otherwise comparable interspecific pairings, snaps were always exchanged (median number = 7) and 60% of the individuals suffered some injury (Knowlton and Keller, 1982, description of the laboratory set-up).

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